Fish communities associated with cold-water corals vary with depth and substratum type

Deep-Sea Research I 114 (2016) 43–54

Contents lists available at ScienceDirect

Deep-Sea Research I

journal homepage: www.elsevier.com/locate/dsri

Fish communities associated with cold-water corals vary with depth and substratum type

Rosanna J. Milligan [a,*], Gemma Spence [a], J. Murray Roberts [b,c], David M. Bailey [a]

[a] Institute of Biodiversity, Animal Health and Comparative Medicine, Graham Kerr Building, University of Glasgow, Glasgow G12 8QQ, UK
[b] Centre for Marine Biodiversity & Biotechnology, School of Life Sciences, Heriot-Watt University, Edinburgh EH14 4AS, UK
[c] Center for Marine Science, University of North Carolina Wilmington, 601 S College Road, Wilmington, NC 28403-5928, USA

ARTICLE INFO

Article history:
Received 25 September 2015
Received in revised form
4 April 2016
Accepted 22 April 2016
Available online 24 April 2016

Keywords:
Deep-sea fish
Cold-water corals
Habitat association
Resource use

ABSTRACT

Understanding the processes that drive the distribution patterns of organisms and the scales over which these processes operate are vital when considering the effective management of species with high commercial or conservation value. In the deep sea, the importance of scleractinian cold-water corals (CWCs) to fish has been the focus of several studies but their role remains unclear. We propose this may be due to the confounding effects of multiple drivers operating over multiple spatial scales. The aims of this study were to investigate the role of CWCs in shaping fish community structure and individual species-habitat associations across four spatial scales in the NE Atlantic ranging from "regions" (separated by > 500 km) to "substratum types" (contiguous). Demersal fish and substratum types were quantified from three regions: Logachev Mounds, Rockall Bank and Hebrides Terrace Seamount (HTS). PERMANOVA analyses showed significant differences in community composition between all regions which were most likely caused by differences in depths. Within regions, significant variation in community composition was recorded at scales of c. 20–3500 m. CWCs supported significantly different fish communities to non-CWC substrata at Rockall Bank, Logachev and the HTS. Single-species analyses using generalised linear mixed models showed that *Sebastes* sp. was strongly associated with CWCs at Rockall Bank and that *Neocyttus helgae* was more likely to occur in CWCs at the HTS. Depth had a significant effect on several other fish species. The results of this study suggest that the importance of CWCs to fish is species-specific and depends on the broader spatial context in which the substratum is found. The precautionary approach would be to assume that CWCs are important for associated fish, but must acknowledge that CWCs in different depths will not provide redundancy or replication within spatially-managed conservation networks.

1. Introduction

Understanding how fish are distributed across marine landscapes is vital in establishing effective management strategies for their conservation and sustainable use. This is particularly true where management is to be largely based on spatially explicit management tools (e.g. Marine Protected Areas (MPAs); FAO, 2007). The deep sea is one such environment, with management measures increasingly targeted towards identifying and protecting Vulnerable Marine Ecosystems (VMEs; e.g. FAO, 2009). In Europe these measures have largely been introduced in response to the requirements of the Habitats Directive (Council Directive 92/43/EEC). Further spatial measures are being implemented due to the Marine Strategy Framework Directive (MFSD; 2008/56/EC), under which a far wider range of species and habitats must be considered through ecosystem-level approaches to management. Unfortunately, relatively little is understood about how deep-sea fish are spatially distributed over the seafloor, and there is therefore an urgent requirement for high quality data to inform management decisions.

Many deep-sea demersal fish species inhabiting the continental slopes (200–4000 m) are targeted by deep-water fisheries or captured as bycatch. Although deep-sea fish show a range of life-history traits (Drazen and Haedrich, 2012), they can be particularly vulnerable to over-exploitation if, for example, they have low fecundity or slow growth rates (Norse et al., 2012). Given the high mobility and potentially broad spatial ranges of deep-sea fish, studies examining their fine-scale distribution patterns are rare, and yet such data are vital in developing appropriate management plans for the conservation and sustainable management of fish stocks. However, if a fish species or community associates strongly

* Corresponding author. Present address: Halmos College of Natural Sciences and Oceanography, NOVA Southeastern University, 8000 North Ocean Drive, Dania Beach, FL 33004, USA.
E-mail address: R.Milligan@nova.edu (R.J. Milligan).

http://dx.doi.org/10.1016/j.dsr.2016.04.011

with particular habitat features, then it may be possible to use those features as surrogates for fish distributions (e.g. Anderson et al., 2009). If those features are themselves of conservation importance, then it may be relatively simple to extend existing management objectives to include the requirements of the fish species.

Framework-forming cold-water corals (CWCs) are colonial, ahermatypic scleractinians and one of the most widespread taxa in the deep oceans (Roberts et al., 2006; Roberts et al., 2009). CWCs have a circumglobal distribution defined predominantly by depth, temperature and water chemistry (Roberts et al., 2006; Davies and Guinotte, 2011), and are believed to increase benthic habitat heterogeneity and biological diversity by providing "islands" of complex, hard substrata in an environment otherwise dominated by soft sediments (Buhl-Mortensen et al., 2010). However, as well as being ecologically valuable, CWCs are highly vulnerable to trawl damage (Hall-Spencer et al., 2002; Althaus et al., 2009). CWCs have therefore been recognised as VMEs and are a target of global conservation efforts in the High Seas (e.g. de Juan and Lleonart, 2010; Rengstorf et al., 2013). In European waters, they are listed as Annex 1 habitats under the Habitats Directive. If CWCs provide important substrata for deep-sea fish, closures to protect CWCs may also be a useful tool for the management of those species.

Despite increasing interest in understanding the importance of CWCs to fish, results published to date remain equivocal. In Norwegian waters, Mortensen et al. (1995) and Fosså et al. (2002) reported higher abundances of redfish (*Sebastes* spp.) over coral bioherms. Husebø et al. (2002) used long-lines and gillnets to capture higher numbers of redfish where CWCs were present, as well as larger sizes of redfish (*Sebastes* spp.), ling (*Molva molva*) and tusk (*Brosme brosme*) compared to areas where CWCs were absent, while Kutti et al. (2014) caught higher numbers of several commercially-important fish species where CWCs were present. Costello et al. (2005) used a range of methodologies to study fish associations with CWCs across eight regions of the NE Atlantic and found that although depth was the strongest predictor of community composition across the entire study area, areas containing CWCs generally supported a different fish fauna to those without CWCs, with a number of species-specific associations occurring within different regions. Soeffker et al. (2011) conducted two ROV video surveys across the Giant and Twin coral mounds (NE Atlantic), but only detected a significant effect of substratum type at the Giant Mound. Again however, they noted a small number of significant species-specific associations with CWCs. In the NW Atlantic, Ross and Quattrini (2007) provided one of the clearest demonstrations of CWC association by deep-water fish, reporting a unique and possibly obligate fish fauna occurring on coral mounds on the Blake Plateau. In the NE Pacific, Du Preez and Tunnicliffe (2011) reported close associations between *Sebastes* spp. and both CWCs and emergent epifauna (e.g. gorgonians and sponges).

Not all studies have demonstrated associations between CWCs and fish however. A long-term video study of individual species associations with CWCs in the Belgica Mound province of the NE Atlantic found no differences in either the abundance or biomass of fish associated with CWCs. Instead, physical variables such as depth were cited as the main predictors of distribution, though effects varied between sites (Biber et al., 2014). Long-lining (D'Onghia et al., 2012) and towed-video surveys (D'Onghia et al., 2011) conducted in the Santa Maria de Leuca CWC province in the Mediterranean Sea found no significant effect of CWCs on the overall fish community, though it was suggested that some taxa may use CWCs preferentially at different life stages. In the NW Atlantic, Auster (2005) found that coral substrata in the Gulf of Maine were functionally indistinguishable from substrata created by other large epifauna and did not support a distinct fish assemblage. Baker et al. (2012) examined fish abundance and community composition in three canyons in the Grand Banks region, but failed to find any association between fish abundance or community composition and CWCs, instead citing depth as the major influence. Stone (2006) noted that apparent associations could arise because certain fish and "habitat-forming" fauna share a preference for similar substrata leading to covariance which may be difficult to separate. The studies considered here include a diverse range of methodologies and taxa and cover a wide geographic range, but when taken together suggest that the distributions of fish within CWC areas may be influenced by a range of processes operating across multiple scales of organisation.

The importance of scale in ecological studies is well known (e.g. Levin, 1992; Chave, 2013). Patterns of both biodiversity (e.g. Levin et al., 2001; Buhl-Mortensen et al., 2010) and the habitat selection choices made by individuals (Morris, 1987; Mayor et al., 2009; Gaillard et al., 2010) are strongly influenced by spatial scale. Following their 2007 study, Ross and Quattrini (2009) determined that faunal associations at the Blake Plateau were driven primarily by depth and habitat structure over regional scales (700 km), though the nature of these relationships varied between sites. At fine scales, Quattrini et al. (2012) determined that other habitat characteristics were important to distributions of fish at the Blake Plateau, and their importance was specific to particular fish species. Linking fine-scale variability in habitat diversity and habitat-use patterns to broader scales that are appropriate for management use is likely to be important in understanding the high variability observed in fish associations with CWCs to date. However, the influence of multiple spatial scales has not yet been examined within a single study, which may lead to difficulties in extrapolating from one study to another due to differences in methodologies and temporal variation.

The aims of the present study were to examine the importance of CWCs in shaping the distribution patterns of demersal fish populations and communities and to determine how they may be influenced by the scale at which the analysis is conducted. The aims are addressed using opportunistically-collected ROV video footage from the NE Atlantic collected over four nested spatial scales and the data are used to provide recommendations for future management of deep-sea fish.

2. Study sites

The distributions of fish were studied in three regions of the NE Atlantic (Fig. 1): the Logachev Mounds (SE Rockall Bank), NW Rockall Bank and the Hebrides Terrace Seamount (HTS; continental slope). CWCs have previously been observed in all regions.

2.1. Logachev Mounds

The Logachev Mounds are located on south-eastern slope of the Rockall Bank, between c. 600–800 m and extend approximately 120 km along the slope edge (Kenyon et al., 2003). The mounds in this region support prolific "framework building reefs" (primarily of *Lophelia pertusa* and *Madrepora oculata*) containing extensive areas of living and dead framework. Parts of the Logachev Mound area have been closed to fishing (EC 41/2006; Fig. 1), but these lie outside the region studied here.

2.2. NW Rockall Bank

Small patches of *Lophelia pertusa* have been recorded from NW Rockall Bank between c. 220–350 m depth (Wilson, 1979a; Howell et al., 2009). Part of this area was closed to fisheries in 2006 (EC 41/2006; Fig. 1) and has since been recognised as an EU Site of

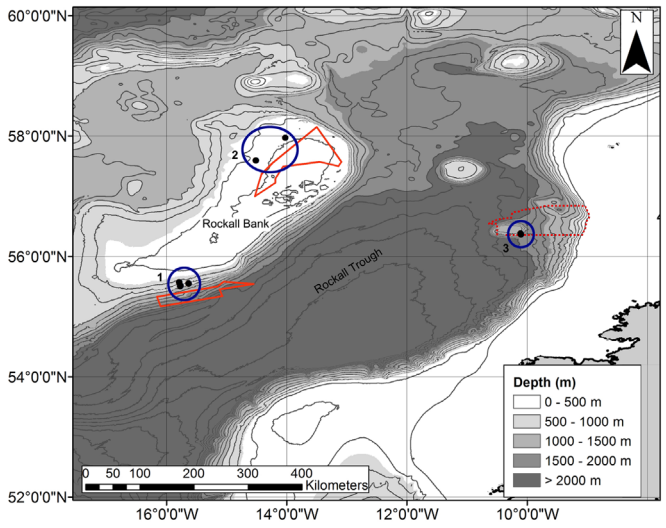

Fig. 1. Map of the study area showing the three regions (circled) and reefs within them. 1. Logachev Mounds, 2. Rockall Bank, 3. HTS. Current closed areas at the Logachev Mounds and NW Rockall Bank are highlighted (solid lines), where fishing with mobile and static gears has been prohibited. The Scottish MPA around the Barra Seafan and HTS is highlighted (dashed line), but no restrictions are currently in force. Contour lines are spaced at 200 m intervals. Chart datum: WGS84.

Community Importance (SCI; UK0030363). The management areas lie outside the region examined here.

2.3. Hebrides Terrace Seamount (HTS)

The HTS is a volcanic guyot on the base of the Scottish continental slope with a maximum depth of 2000–1650 m, and rising to a flat summit at approximately 1000 m (Buckley and Bailey, 1975). Using the same video transects as the present study, Henry et al. (2014) reported the presence of small patches of *Solenosmilia variabilis* and other taxa on the flanks of the HTS. The HTS and Barra seafan have recently been designated as a "Nature Conservation MPA" by the Scottish Government, but no management measures were in place at the time of the study.

3. Materials and methods

Data on the demersal fish were collated from opportunistically-collected high-definition video footage captured during research cruise JC073 (Roberts, 2013) using an Insite Mini Zeus camera mounted on the ROV *Holland I*. In total, 17 ROV transects provided 27 h 7 min of useable video footage covering a total linear distance of 17.9 km (Fig. 2, Table 1). Additional metadata for each transect are provided in Supplement A.

The study area was subdivided according to four nested spatial scales. "Regions" were the broadest scale (c. 175–540 km), and contained a number of "reefs" (5.5–49.5 km). Reefs in turn contained a number of "transects" (containing footage from one ROV survey dive; 20–3400 m) and each transect contained contiguous "substratum patches" (hereafter simply referred to as "patches"). These categories should be considered approximations of spatial scale, as they varied between regions. Notably, the HTS did not contain "reefs" and the distances between transects were greater than in other regions (15.2–16.2 km). Patches were classified according to the dominant substratum type within the total field of view (following Dorschel et al., 2009; Fig. 3) and defined the sampling units and spatial resolution of the study. These classifications could be generalised into "coral reef" substrata (coral thicket, open coral thicket), "transitional" substrata (coral rubble and colonies, coral rubble) or "non-coral" substrata (where scleractinian corals were not observed in the video) following definitions adapted from Costello et al. (2005).

Each transect was initially reviewed by one of two observers to identify the locations of fish fauna and changes in substrate type. Transects were assigned to an observer at random and analysed in a randomised order. Footage was only analysed when the ROV was moving over the seafloor at an approximately steady speed and direction, and when the camera was fully zoomed-out and stable. Footage was excluded where poor visibility prevented detection of the fish fauna, and from periods when the ROV was stationary, moving erratically, or was engaged in other activities. Only transects containing more than five minutes of useable footage were processed. All useable footage was then reviewed and transects divided into discrete patches. The start and end times of each patch were recorded.

Each transect was reviewed a second time and the fish fauna were counted and identified to the highest possible taxonomic resolution based on morphological and behavioural characteristics, following Hureau (1996). Individuals that could not be formally identified to species but that were morphologically distinct from the other taxa were classified as distinct morphotypes (e.g. "Macrouridae sp. 1"). Individuals that could not be identified were classed as "indeterminate species" and excluded from analysis. The time at which each fish was first observed was recorded. Finally, all substratum classifications and species identities were reviewed to remove observer bias.

Time, depth and position of the ROV over the seabed were recorded at two-second intervals using a USBL navigation sensor. The locations and lengths of each patch were calculated by cross-referencing their start and end times to the USBL data. Degrees latitude and longitude were converted to UTM (Northing and Easting) and combined with the depth measurements to describe the ROV's position in metres using an x, y, z grid system. Outliers were manually removed from the 3D position data and the remaining data smoothed using moving averages (N = 10 data points). Any small sections of data which remained erratic (i.e. where the distance travelled was unfeasibly high) were removed and substituted with mean data from neighbouring patches. Estimates of mean depth (m), Northing, Easting and survey speed (m min^{-1}) and length (m) were calculated for each patch. The mean gradient ("slope") of the seafloor was estimated for each patch by dividing the depth range by the horizontal distance travelled. Survey speed was included because it can influence survey error and fish responses towards the ROV (Trenkel et al., 2004). Metadata for each survey are available through the British Oceanographic Data Centre (Milligan et al., 2016).

3.1. Data analysis

Fish community structure was analysed using non-metric multivariate comparisons of community composition within and between sample groups using patches as the sampling units. Since the three regions were spatially distinct from each other (Fig. 2) and did not always have the same nested structure (i.e. the HTS did not contain "reefs"), all analyses were conducted in two stages. The first examined the broad-scale effects of "region" on community structure, and the second stage examined the finer-scale variation within each region separately.

Multivariate analyses were conducted using PRIMER 6 software with PERMANOVA (Clarke and Gorley, 2006). Multivariate results were considered significant at $p < 0.05$. Samples that contained no fish were excluded as they would strongly bias the results. Fish counts were standardised by patch length to control for differences in survey effort between different patches and produce an estimate of relative abundance (N m^{-1}). While this approach does

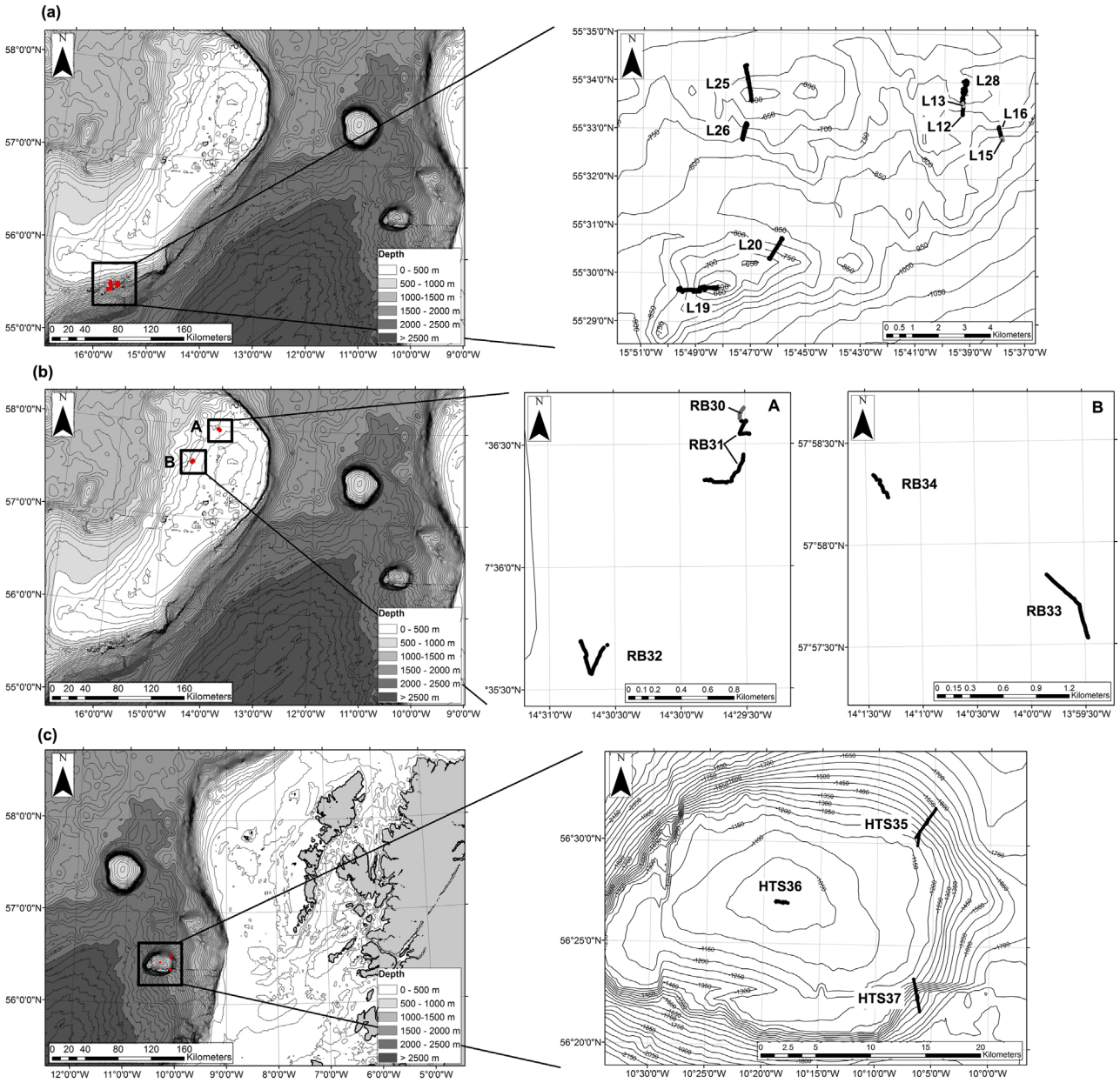

Fig. 2. Locations of the ROV transects conducted at (a) Region 1: Logachev, (b) Region 2: Rockall Bank, (c) Region 3: HTS. Gaps in the transects indicate where unusable footage was removed prior to analysis. Projection: UTM Zone 28U (a) & (b); UTM Zone 29U (c) & (d).

not account for fine-scale spatial autocorrelation between neighbouring patches, it will nonetheless allow us to examine general patterns of fish associations with CWCs over the total study area. The relative abundances were then multiplied by 1000 for ease of presentation and analysis. Scaling in this manner has no effect on the analytical outputs. However, the abundances should not be extrapolated beyond the spatial limits of the present study as they may not be accurate over broader spatial scales. Finally, the data were square-root transformed prior to analysis. Bray-Curtis similarity matrices were generated to analyse the relative abundance data, and Euclidian distance matrices for the environmental data. Six outliers, each containing a single individual from a unique species, were identified using non-metric Multi-Dimensional Scaling (nMDS) and removed to avoid biasing the results.

PERMutational ANalysis Of VAriance (PERMANOVA; Anderson, 2001) was used to test the effects of substratum type and environmental variables on community composition. The effects of "region" were tested separately from the environmental variables because depth and location covaried with region. For analyses within each region, substratum type was included as a fixed effect nested within "transect" (random effect), which was nested within "reef" (random effect) as appropriate. Environmental data were included as covariates. Latitude and longitude were excluded from analyses conducted within regions, because they were not considered to be biologically meaningful at these spatial scales. In all cases, sequential (type I) sums of squares were used as appropriate for nested data with covariates, and environmental terms were included before substratum terms. Models were permuted 9999 times under a reduced model. Backwards model selection was used to produce the fitted model from the saturated model. Pairwise comparisons were used to identify where significant differences occurred between factor levels, using Monte-Carlo sampling if the number of unique permutations was too small to allow calculation of p-values by permutation. Where significant differences were identified, PERMDISP analysis (Anderson, 2006) was used to determine whether these differences could have been caused by

Table 1
Summary data for each ROV transect.

Transect no.	Date	Region	Reef	No. patches	Total transect length (m)	Mean patch length (m) (± 1 S.D.)	Mean patch depth (m) (Min., Max.)	Mean survey speed (m/min) (± 1 sD.)
L12	27/05/2012	Logachev	Logachev 1	7	432.2	61.7 (± 93.5)	686.7 (717.9, 598.3)	9.0 (± 2.3)
L13	27/05/2012	Logachev	Logachev 1	1	63.8	63.8	560.3 (560.3, 560.3)	6.4
L15	28/05/2012	Logachev	Logachev 1	2	25.7	12.9 (± 2.3)	873.1 (873.3, 872.9)	7.8 (± 3.5)
L16	28/05/2012	Logachev	Logachev 1	53	536.1	10.1 (± 26.1)	819.5 (872.5, 752.3)	8.5 (± 3.2)
L19	30/05/2012	Logachev	Logachev 2	126	1448.6	11.5 (± 18.4)	684.3 (833.6, 552.6)	9.9 (± 2.9)
L20	30/05/2012	Logachev	Logachev 2	110	995.3	9.0 (± 22.1)	738.9 (865.5, 591.9)	12.2 (± 3.7)
L25	04/06/2012	Logachev	Logachev 3	123	1357.6	11.1 (± 31.1)	595.7 (688.2, 538.3)	11.8 (± 3.3)
L26	04/06/2012	Logachev	Logachev 3	63	499.9	7.9 (± 7.3)	728.8 (768.0, 693.2)	10.7 (± 3.3)
L28	06/06/2012	Logachev	Logachev 1	68	478.4	7.0 (± 9.3)	632.4 (671.3, 564.5)	9.2 (± 2.5)
RB30	07/06/2012	Rockall Bank	Pisces 9	6	89.7	14.9 (± 11.4)	255.4 (254.7, 256.7)	12.5 (± 2.7)
RB31	07/06/2012	Rockall Bank	Pisces 9	47	673.5	14.3 (± 14.9)	256.0 (252.5, 259.1)	9.7 (± 4.5)
RB32	07/06/2012	Rockall Bank	Pisces 9	28	230.8	8.3 (± 8.1)	261.8 (259.4, 264.2)	4.3 (± 2.3)
RB33	08/06/2012	Rockall Bank	NW Rockall Bank	36	701.6	19.5 (± 16.8)	219.4 (217.5, 222.3)	8.4 (± 2.5)
RB34	08/06/2012	Rockall Bank	NW Rockall Bank	24	252.1	11.3 (± 11.0)	223.2 (220.0, 226.0)	11.7 (± 4.8)
HTS35	09/06/2012	HTS	Seamount	192	5130.5	66.6 (± 169.2)	1481.8 (1657.8, 1241.8)	14.3 (± 3.3)
HTS36	10/06/2012	HTS	Seamount	23	1371.7	59.6 (± 117.6)	993.0 (998.9, 982.2)	10.9 (± 2.4)
HTS37	10/06/2012	HTS	Seamount	54	3595.6	26.7 (± 145.6)	1403.4 (1603.2, 1221.9)	12.2 (± 3.3)

differences in the multivariate dispersion of points rather than their location. SIMilarity PERcentages (SIMPER) analysis was used to determine which species contributed most to any significant results.

Within each region, differences in environmental variables between substrata were tested using linear models (LM) in R software (Version 3.1.0, R Core Team, 2014). The effects of substratum type and the other environmental variables were tested on the patch occupancy (*PO*; a binary response) and raw counts (N) of the dominant fish taxa using Generalised Linear Mixed Models (GLMMs). All samples were included in these analyses, including those that contained no fish. "Transect" was included as a random effect and "substratum type" , "survey speed" , "slope" ($\log_e$ transformed), "reef" and "depth" were included as fixed effects as appropriate (Eq. (1)). "Reef" could not be included as a random effect as it contained too few levels to produce valid results (Bolker et al., 2009). "Patch length" was included as an offset term. Fish counts were modelled using packages "glmmadmb" (Fournier et al., 2012). Patch occupancy (Eq. (2)) was modelled using "lme4" (Bates et al., 2015) in R software.

$$Log_e(N) = substratum\ type + log_e(slope) + depth + speed + reef + (1|transect) + offset(log_e(patch\ length)) \quad (1)$$

$$logit(PO) = substratum\ type + log_e(slope) + depth + speed + reef + (1|transect) + offset(log_e(patch\ length)) \quad (2)$$

Model selection for the count data was carried out in two stages. First, the suitability of different distributions (Poisson (P), negative binomial (NB), zero-inflated Poisson (ZIP) and zero-inflated negative binomial (ZINB)) was assessed for the saturated model using AIC. Second, backwards-selection of model terms was used to produce the fitted model. The significance of each term was assessed using likelihood-ratio testing and non-significant variables were removed. Since p-values generated in this way are approximate (Bolker et al., 2009), GLMM terms were only considered to have a significant effect if $p < 0.01$. Model validation was carried out by plotting Pearson's residuals against both the fitted values and against each of the explanatory variable included in the fitted model. Predicted counts were also plotted against observed counts. Similar model selection and validation procedures were conducted for the patch occupancy analyses, with the exception that patch occupancy was always modelled using a binomial distribution.

4. Results

Analysis of the useable footage revealed a total of 1949 identifiable fish (plus 80 indeterminate individuals) from 57 taxa (Table 2). A morphotype catalogue is provided in Supplement B.

4.1. Broad-scale patterns

4.1.1. Environmental data

The environmental characteristics of the three regions showed significant differences. All regions were spatially distinct from each other and occurred at different depths (Table 1). The steepest seabed slopes occurred at Logachev and the flattest at NW Rockall Bank (LM: $F=111.8$, $DF=2$, $p<0.0001$). ROV survey speed also varied significantly between regions by c. 4 m min^{-1} (LM: $F=95.45$, $DF=2$, $p<0.0001$), with the highest average speeds occurring at the HTC and the lowest at Rockall Bank.

4.1.2. Community data

Multivariate analysis of the total fish community showed that region (PERMANOVA: Pseudo-$F=59.0$, $DF=2$, $p=0.0001$; Fig. 4(a)),

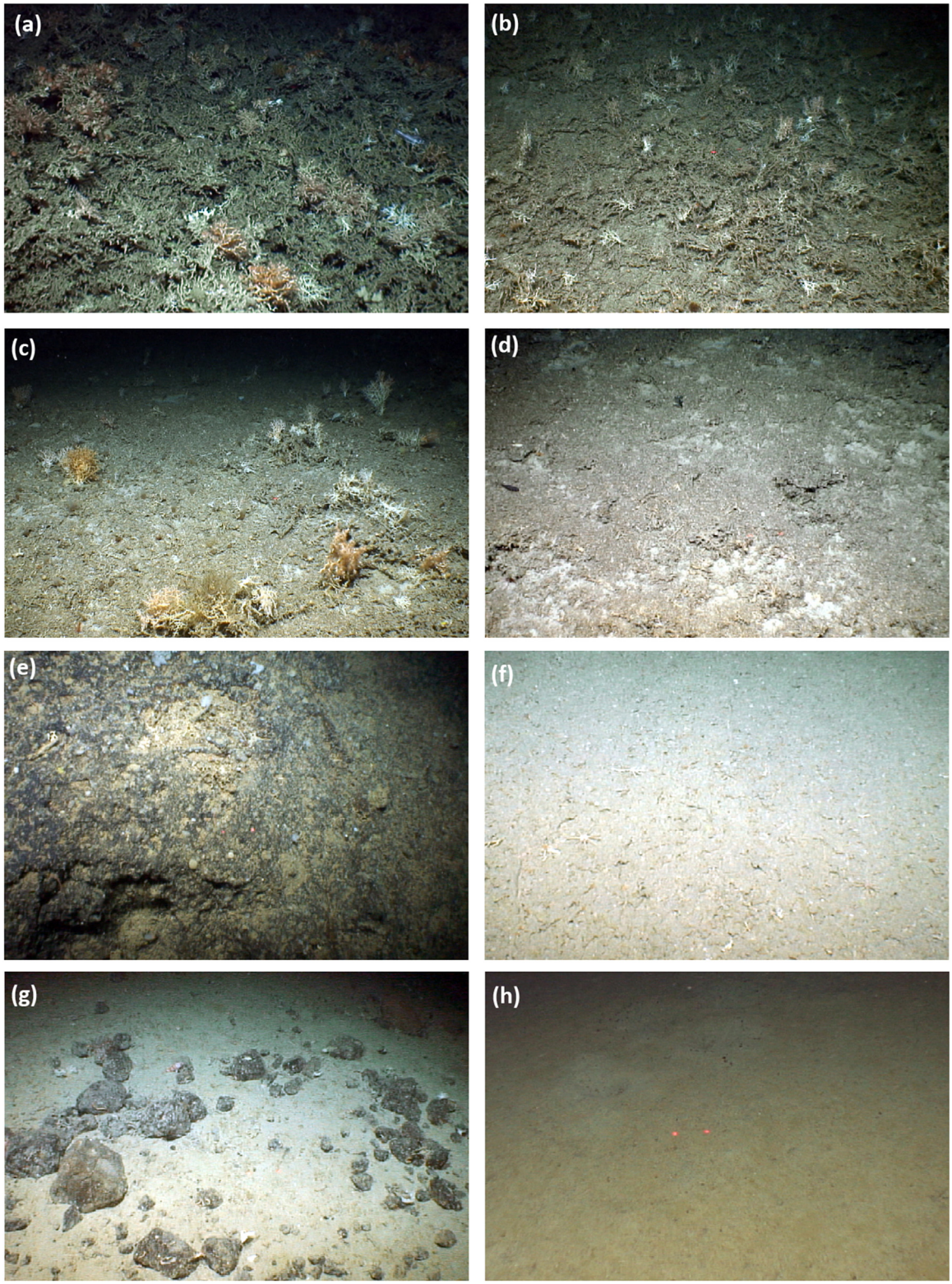

Fig. 3. Examples of each substratum type. (a) Coral thicket, (b) Open coral thicket, (c) Coral rubble and colonies, (d) Coral rubble, (e) Hard ground (bedrock), (f) Consolidated sediment, (g) Soft sediment and stones, and (h) Soft sediment.

had a significant effect on the fish composition. nMDS plots visualising the effects of depth (Fig. 4(b)), latitude (Fig. 4(c)) and longitude (Fig. 4(d)) show a progressive change in community composition that best correlates with depth. SIMPER analysis indicated that the similarity between samples taken from the same region was greater than between samples from different regions (Table 3).

4.1.3. *Dominant species*

Although similarities in fish composition within regions were relatively low (SIMPER: 19.28–28.9%), each region could be defined by a small number of dominant taxa (Table 4). Gadoids and *Sebastes* sp. 1 dominated at NW Rockall Bank, while morids and macrourids dominated the Logachev Mounds and HTS fauna.

Table 2
Fish taxa observed within each region. Raw counts (N) and standardised counts (N m^{-1}) are provided for each taxon. Taxa for which fisheries landings data are available from the FAO database (FAO, 2009) are highlighted (species data=*; family data=†).

Fish Taxon	Region	Logachev Mounds		Rockall Bank		Hebrides Terrace Seamount	
	Authority	Raw counts (N)	Standardised counts (N m^{-1}) × 1000	Raw counts (N)	Standardised counts (N m^{-1}) × 1000	Raw counts (N)	Standardised counts (N m^{-1}) × 1000
Alepocephalidae sp. 1		0	0.0	0	0.0	3	5.9
Anguilliformes spp.		2	159.5	0	0.0	22	186.2
Angulliforme sp. 1		15	711.8	0	0.0	0	0.0
*Antimora rostrata**	(Günther, 1878)	0	0.0	0	0.0	1	10.7
*Brosme brosme**	(Ascanius, 1772)	0	0.0	1	70.2	0	0.0
*Chimaera monstrosa**	Linnaeus, 1758	3	150.5	0	0.0	2	16.8
Chimaera spp.†	Linnaeus, 1758	0	0.0	0	0.0	2	23.0
Chondrichthyes sp. 1		2	10.3	0	0.0	0	0.0
Chondrichthyes sp. 2		1	4.6	0	0.0	0	0.0
Chondrichthyes sp. 3		1	54.2	0	0.0	0	0.0
Chondrichthyes sp. 4		0	0.0	0	0.0	7	334.3
Coelorhynchus caelorhynchus	(Risso, 1810)	106	9250.1	0	0.0	0	0.0
Coelorhynchus labiatus	(Köhler, 1896)	0	0.0	0	0.0	83	839.8
Coryphaenoides armatus	(Hector, 1875)	0	0.0	0	0.0	1	0.9
*Coryphaenoides rupestris**	Gunnerus, 1765	0	0.0	0	0.0	32	1123.4
Epigonus sp. 1		0	0.0	0	0.0	4	3.7
Gadidae sp. 1		0	0.0	290	24,452.8	0	0.0
Gadiformes sp. 1		0	0.0	17	3168.8	0	0.0
Gaidropsarus sp.	Rafinesque, 1810	10	277.6	0	0.0	0	0.0
Guttigadus latifrons	(Holt & Byrne, 1908)	1	92.3	0	0.0	0	0.0
Halosauridae spp.		0	0.0	0	0.0	12	196.3
Halosauridae sp. 1		0	0.0	0	0.0	2	410.2
Halosauridae sp. 2		0	0.0	0	0.0	13	116.3
Halosauridae sp. 3		1	67.2	0	0.0	0	0.0
*Helicolenus dactylopterus**	(Delaroche, 1809)	141	16,307.1	127	15,875.3	0	0.0
Hydrolagus mirabilis†	(Collett, 1904)	0	0.0	0	0.0	5	9.4
Lepidion eques	(Günther, 1887)	295	26,313.2	0	0.0	73	2759.2
Lophius sp.†	Linnaeus, 1758	1	102.4	0	0.0	0	0.0
Lotidae spp.		1	70.7	0	428.0	2	38.1
Macrouridae spp.	Gilbert & Hubbs, 1916	16	2763.7	0	0.0	33	961.6
cf. *Malacoraja kreffti*	(Stehmann, 1978)	0	0.0	0	0.0	2	31.0
*Micromesistius poutassou**	(Risso, 1827)	1	685.5	43	1604.5	0	0.0
*Molva dypterygia**	(Pennant, 1784)	13	243.4	5	583.7	0	0.0
*Molva molva**	(Linnaeus, 1758)	0	0.0	9	530.2	0	0.0
Molva spp.	Lesueur, 1819	0	0.0	7	642.6	1	2.1
*Mora moro**	(Risso, 1810)	6	504.6	0	0.0	0	0.0
Moridae spp.	Moreau, 1881	29	2924.0	0	0.0	1	10.3
Neocyttus helgae	(Holt & Byrne, 1908)	1	6.7	0	0.0	64	4630.9
*Phycis blennoides**	(Brünnich, 1768)	1	164.5	3	115.2	0	0.0
Pleuronectiformes sp. 2		0	0.0	36	1476.0	0	0.0
Pleuronectiformes sp. 3		0	0.0	1	30.3	0	0.0
*Pollachius virens**	(Linnaeus, 1758)	0	0.0	1	18.3	0	0.0
Scorpaenidae spp.		1	182.1	0	0.0	0	0.0
Sebastes sp. 1*		0	0.0	238	18,571.7	0	0.0
Synaphobranchidae sp.		0	0.0	0	0.0	1	0.9
Synaphobranchus kaupii	Johnson, 1862	1	92.3	0	0.0	44	491.2
Trachyscorpia cristulata cristulata	(Goode & Bean, 1896)	2	324.3	0	0.0	0	0.0
Teleostei sp. 1		0	0.0	0	0.0	3	1.3
Indet.		80	11,027.6	26	2572.3	66	2280.0
Regional total		**731**	**72,490.2**	**804**	**70,139.9**	**479**	**14,483.5**

Close-up views of *Sebastes* sp. 1 suggested that this species was likely to be *Sebastes viviparus*, though it could only be consistently identified to morphotype.

4.2. Intermediate and fine-scale patterns

4.2.1. Region 1: Logachev Mounds

4.2.1.1. General description. The CWCs at Logachev comprised extensive banks of *Lophelia pertusa*, and had the highest proportion of coral cover of any of the regions, with coral reef and transitional substrata comprising between 70.4% (Logachev 3) and 98.7% (Logachev 1) of the total surveyed substrata. Coral reef substrata were more likely to occur at shallower depths (LM: $F=74.7$, $DF=12$, $p<0.01$) and on steeper slopes (LM: $F=10.06$, $DF=12$, $p<0.01$) than transitional and non-coral substrata. Other emergent epifauna (e.g. Alcyonacea) were observed but not recorded in the present study.

4.2.1.2. Community data. A total of 731 individual fish were observed (Table 2). Substratum type (PERMANOVA: Pseudo-$F=1.69$, $DF=25$, $p=0.0007$; Fig. 5(a)) and depth (PERMANOVA: Pseudo-$F=18.577$, $p<0.001$) had significant effects on community composition. No significant difference in multivariate dispersion was

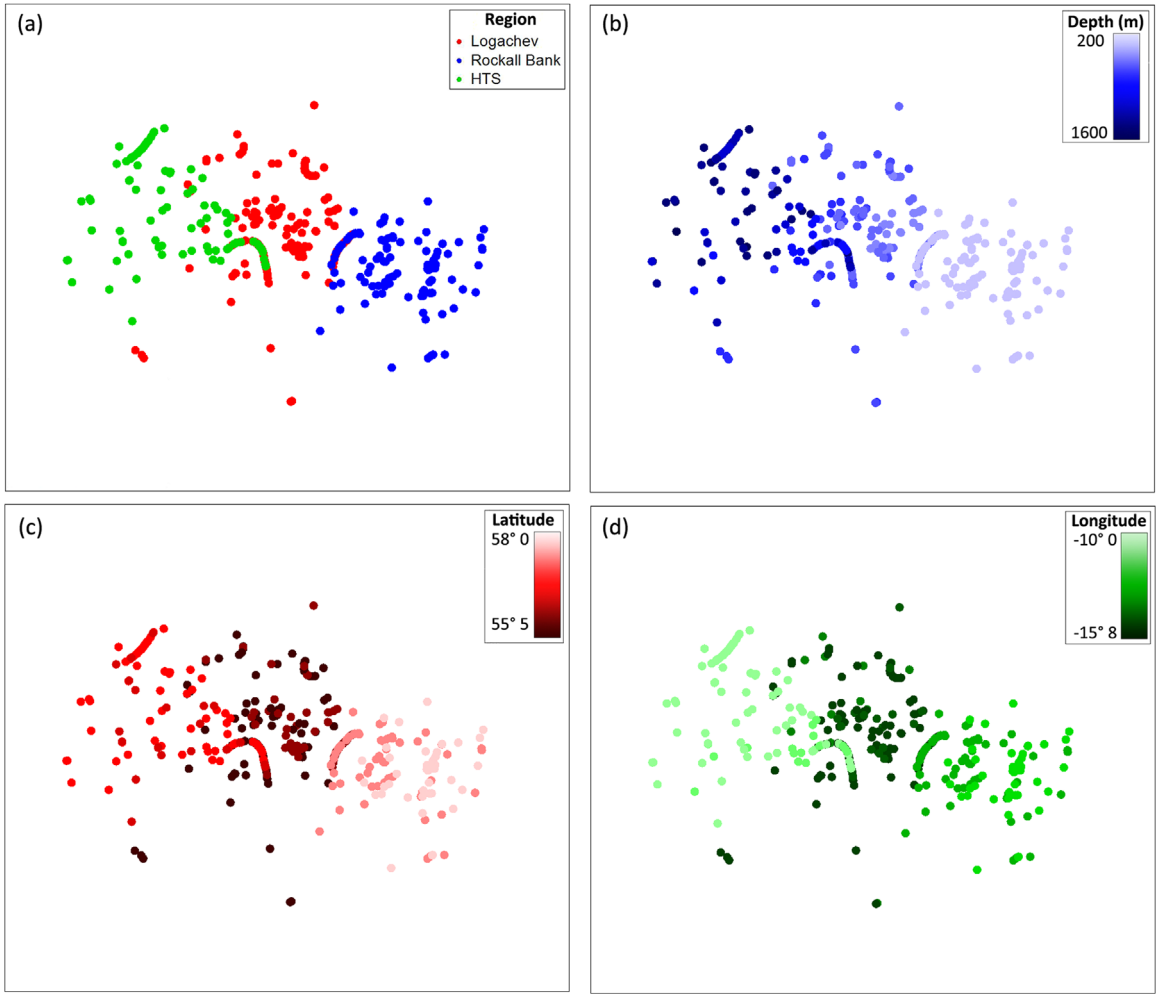

Fig. 4. nMDS showing the differences in assemblage composition (a) between regions (ANOSIM: $p < 0.001$); (b) with depth (BIOENV: $p < 0.001$), (c) with latitude (BIOENV: $p < 0.001$), (d) with longitude (BIOENV: $p < 0.01$). Each point represents one patch. For clarity, three outlying points are not shown. Data have been square-root transformed and distances are based on Bray-Curtis similarity. Stress = 0.05.

Table 3
Mean Bray-Curtis similarity between regions.

	Logachev Mounds	Rockall Bank	HTS
Logachev Mounds	28.48		
Rockall Bank	7.41	28.40	
HTS	9.11	0.01	18.98

Table 4
Mean standardised abundance (N m^{-1} (x1000); ± 1 S.D.) of characteristic taxa from each region. Blank cells indicate zeros.

	Logachev Mounds	Rockall Bank	HTS
Lepidion eques	106.1 (± 156.16)		28.15 (± 67.06)
Helicolenus dactylopterus	65.75 (± 132.94)	144.3 (± 245.04)	
Coelorhynchus caelorhynchus	37.3 (± 89.65)		
Gadidae sp. 1		222.3 (± 490.50)	
Sebastes sp. 1		168.8 (± 506.20)	
Neocyttus helgae			47.25 (± 76.69)
Coelorhynchus labiatus			8.57 (± 29.93)
Macrouridae sp.			9.81 (± 30.98)

detected between substratum types (PERMDISP: $F = 0.35$, $DF = 5$, $p > 0.05$). Significant variation between transects was detected (PERMANOVA: Pseudo-$F = 2.51$, $DF = 6$, $p < 0.001$) but not between reefs (PERMANOVA: Pseudo-$F = 0.78$, $DF = 2$, $p > 0.05$). Interactions between substratum type and slope and depth were tested but none were significant (PERMANOVA: $p > 0.05$). The order in which the variables were entered into the model did not affect the significance of the results.

SIMPER analysis indicated that higher counts of *Coelorhynchus caelorhynchus* (Macrouridae), *Helicolenus dactylopterus* (Scorpaenidae) and *Lepidion eques* (Moridae) occurred in coral reef and transitional substrata, while non-coral substrata contained higher numbers of Anguillidae and Halosauridae.

4.2.1.3. Single species trends. Three species accounted for over 80% of the fish community at the Logachev Mounds: *Lepidion eques* (43%), *Coelorhynchus caelorhynchus* (26.8%) and *Helicolenus dactylopterus* (14.6%). *Lepidion eques* occurred on all substratum types and in all transects, but none of the modelled terms had a significant effect on *L. eques* abundance ($p > 0.05$). Survey speed had a significant, negative effect on the probability of *L. eques* patch occupancy (GLMM (speed): $Chi^2 = 9.54$, $DF = 1$, $p < 0.001$), though the magnitude of the effect was weak (coefficient = −0.1, S.D. = 0.03). No variables had significant effects on the relative abundance or probability of patch occupancy of *Coelorhynchus*

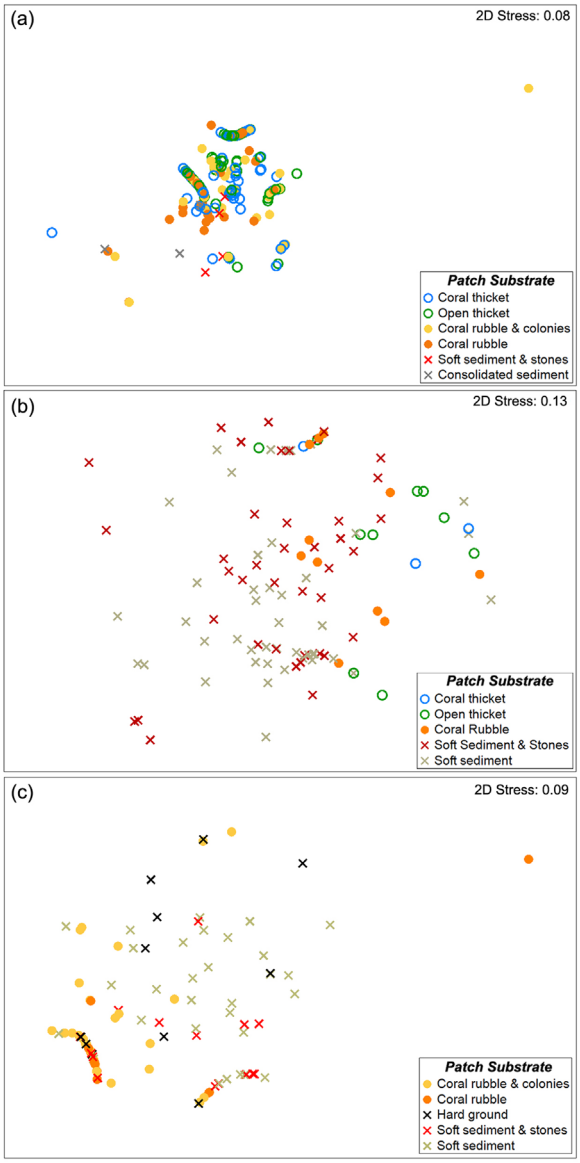

Fig. 5. nMDS plots showing the significant effects of substratum type ($p < 0.05$) on fish community composition at (a) the Logachev Mounds; (b) Rockall Bank and (c) HTS based on Bray-Curtis similarity. Data have been square-root transformed and distances are based on Bray-Curtis similarity. Reef substrata are indicated by closed circles, transitional substrata by open circles and non-coral substrata by crosses.

caelorhynchus ($p > 0.01$). A weak, but significant negative effect of depth (coefficient = −0.02, S. D. = 0.002) on *Helicolenus dactylopterus* abundance (GLMM (depth): Deviance = 111, DF = 1, $p < 0.001$) and patch occupancy (GLMM (depth): $Chi^2 = 80.1$, DF = 2, $p < 0.001$) was observed.

4.2.2. Region 2: Rockall Bank

4.2.2.1. General description. Rockall Bank was dominated by soft sediment and soft sediment and stones, which comprised between 69.9% and 95.3% (mean = 84.9%) of the total substrata in each transect. Coral substrata typically occurred as small thickets of *Lophelia pertusa* ("Wilson rings"; Wilson, 1979b). Water depth varied by approximately 25 m between reefs sites with no overlap (Table 1) and so was excluded from the analyses. Slope and speed varied significantly with substratum type, with CWC substrata associated with steeper slopes than non-coral substratum (LM: F = 4.7, DF = 4, $p < 0.02$) although this appeared to be caused by the vertical relief of the CWCs. Coral rubble was surveyed more slowly than other substratum types.

4.2.2.2. Community data. A total of 839 fish were identified from 16 taxa (Table 2). Substratum type (PERMANOVA: Pseudo-F = 1.41, DF = 14, $p < 0.05$; Fig. 5(b)), slope (PERMANOVA: Pseudo-F = 2.70, $p < 0.05$) and survey speed (PERMANOVA: Pseudo-F = 2.70, $p < 0.05$) were found to have significant effects on community composition, although the significance of slope and speed disappeared if they were included after substratum type in the model. No significant difference in multivariate dispersion was detected between substratum types (PERMDISP: Pseudo-F = 0.367, DF = 4, $p < 0.05$). Significant variation was detected between both transects (PERMANOVA: Pseudo-F = 2.06, DF = 3, $p < 0.01$) and reefs (PERMANOVA: Pseudo-F = 4.30, DF = 1, $p < 0.0001$). Interactions between substratum type and slope were tested but were not significant.

SIMPER analysis indicated that higher counts of *Sebastes* sp. 1 (Scorpaenidae) occurred in coral reef substrata, while higher numbers of *Helicolenus dactylopterus* (Scorpaenidae) and Gadidae sp. 1 occurred in transitional substrata, though both were present in non-coral substrata. Differences between transects and reefs appeared to be driven primarily by differences in the relative abundances of common taxa, rather than by a different in species composition.

4.2.2.3. Individual species trends. Three species accounted for over 80% of the total fish at Rockall Bank: Gadidae sp. 1 (36.4%), *Sebastes* sp. 1 (27.6%) and *Helicolenus dactylopterus* (22.7%). Close-up observations of *Sebastes* sp. 1 suggested that this morphotype was likely *Sebastes viviparus* and indicated the presence of some gravid individuals. One gravid specimen was recovered using a suction sampler. No variables had significant effects on the relative abundance or probability of patch occupancy of Gadidae sp. 1 ($p > 0.01$). Significantly higher counts of *Sebastes* sp. 1 were observed in open coral thicket than in any other substratum (GLMM (substratum): z-value = 3.17, $p < 0.01$). Slope also had a significant, positive effect (GLMM (slope): z-value = 3.17, $p < 0.01$). No variables affected the probability of *Sebastes* sp. 1 patch occupancy (GLMM: $p > 0.01$). No variables had significant effects on the relative abundance or probability of patch occupancy of *Helicolenus dactylopterus* ($p > 0.01$).

4.2.3. Region 3: Hebrides Terrace Seamount

4.2.3.1. General description. The HTS contained extensive areas of apparent soft sediment with gravel (classified as soft sediment). Occasional patches of hard ground were observed on the flanks (HTS 35 and HTS 37). CWC substrata were rare and comprised small *Solenosmilia variabilis* colonies and coral rubble on the flanks of the seamount. Other emergent epifauna (e.g. Alcyonacea) were observed on the flanks of the seamount but not recorded in the present study. Depth was a significant predictor of substratum types on the flanks, with hard ground and soft sediment and stones occurring in shallower depths than other substrata (LM: F = 5.7, DF = 5, $p < 0.01$). Hard ground was significantly steeper, and soft sediment flatter, than other substrata (LM: F = 2.5, DF = 4, $p < 0.05$).

4.2.3.2. Community data. A total of 483 fish were identified from 25 taxa (Table 2). Substratum type (PERMANOVA: Pseudo-F = 1.45, DF = 9, $p < 0.05$; Fig. 5(c)) and depth (PERMANOVA: Pseudo-F = 5.62, $p < 0.01$) were found to significantly affect community composition. Significant differences in multivariate dispersion were detected between substratum types (PERMDISP: F = 3.68, $p < 0.03$) and significant variation was detected between transects (PERMANOVA: Pseudo-F = 8.51, DF = 2, p = 0.0001). SIMPER analysis suggested that differences between substrata were driven by a

greater relative abundance of *Neocyttus helgae* (Oreosomatidae) over transitional than non-coral substrata, and fewer *Lepidion eques* over soft sediment than other substrata. The macrourids *Coryphaenoides rupestris* and *C. labiatus* appeared to be more abundant over soft sediments than other substrata. Indeterminate macrourids, halosaurs and anguillids also contributed to the differences between substratum types.

4.2.3.3. Individual species trends. Six taxa accounted for over 80% of the total standardised fish abundance, excluding unidentifiable species. These were: *Neocyttus helgae* (37.8%), *Lepidion eques* (22.5%), *Coryphaenoides rupestris* (9.2%), Macrouridae spp. (7.9%) and *Coryphaenoides labiatus* (6.9%). Macrouridae spp. was excluded from further analysis as it was not a mono-specific group.

No variables had significant effects on the relative abundance of *Neocyttus helgae*, although it was significantly more likely to occur over transitional substrata than other types (GLMM (substratum): $Chi^2 = 18.6$, $DF = 4$, $p < 0.001$). *Lepidion eques* was significantly more abundant (GLMM: Deviance = 24.7, $DF = 1$, $p < 0.001$), and more likely to occupy shallower depths (GLMM: $Chi^2 = 20.0$, $DF = 1$, $p < 0.001$). *Coryphaenoides rupestris* was significantly more abundant (GLMM: Deviance = 7.7, $DF = 1$, $p < 0.01$) and likely to occur (GLMM: $Chi^2 = 8.0$, $DF = 1$, $p < 0.01$) at greater depths, though the effects were weak (coefficients = 0.005 and 0.007 respectively). No variables had significant effects on the relative abundance or probability of patch occupancy of *Coryphaenoides labiatus*.

5. Discussion

Differences in community composition appeared to be influenced by different variables operating over different spatial scales. At the broadest scales (175–550 km), significant differences in fish community composition were correlated with depth. The importance of depth in structuring deep-sea faunal communities is well-known (e.g. Carney, 2005), and correlations with alpha and beta biodiversity have been demonstrated for north Atlantic fish fauna in general (e.g. Koslow, 1993; Priede et al., 2010; Bergstad, 2013) as well as specifically within CWC regions (Costello et al., 2005; Ross and Quattrini, 2009). While depth per se is unlikely to be the causal driver of these changes because it either directly influences or varies with other physical mechanisms that influence fish distributions (e.g. water mass structure, temperature, light levels, pressure or food supply; Koslow, 1993; Carney, 2005; Bergstad, 2013), it nonetheless provides a useful proxy measure that could be incorporated into a management framework relatively easily (Howell, 2010).

Significant variation in community composition was detected at intermediate spatial scales (c. 5.5–49.5 km) between transects in all regions and between reefs at Rockall Bank. These are similar to findings by Ross and Quattrini (2009) and Quattrini et al. (2012) from the NW Atlantic. The constraints of the present study meant it was not possible to determine whether these differences were driven by underlying environmental variability, or whether they were the result of stochastic variation caused by the low densities of deep-sea fish. Future work should be designed to allow for intermediate-scale variation, either through robust experimental design or appropriate statistical methodologies (e.g. the incorporation of random effects).

At fine scales (20–3400 m) CWCs supported a significantly different fish fauna to non-CWC substrata. The clearest example of this occurred at Rockall Bank, where *Sebastes* sp. 1 (which included some gravid individuals) was closely associated with CWC reef substrata. Links between *Sebastes* spp. and CWCs have been previously reported from the NE Atlantic (e.g. Mortensen et al., 1995; Fosså et al., 2002; Freiwald et al., 2002; Costello et al., 2005), and Foley et al. (2010) recommended that CWCs should be considered "essential fish habitat" for the genus in Norwegian waters. However, while *Sebastes* spp. do associate with CWCs, the relative importance of CWCs compared to other biogenic substrata (formed by Porifera or Alcyonacea for example) is not clear. In the NW Atlantic and NE Pacific for example, *Sebastes* spp. associates with both soft corals (e.g. gorgonians) and CWCs (Stone, 2006; Du Preez and Tunnicliffe, 2011; Miller et al., 2012). In the present study, only 24% of *Sebastes* sp. 1 were observed over non-CWC substrata, strongly suggesting that CWCs were important to this species in the NW Rockall Bank region, at least at the time of the study. Gravid *Sebastes* spp. were observed in association with CWCs in the present study. Similar associations between *Sebastes* spp. and CWCs have been reported by Costello et al. (2005) and Fosså et al. (2002), and with seapens by Baillon et al. (2012) during May and June. Evidence that larval fish were taking refuge within seapens was interpreted by Baillon et al. (2012) as important habitat use. If *Sebastes* sp.1 is reliant on CWCs for all or part of its life cycle, then they may be predicted to be more vulnerable to environmental disturbance and habitat loss than more generalist species (Wilson et al., 2008). Studies at other times of year are lacking however, and the importance of CWCs to population processes have not yet been quantified.

Substratum preferences were less clearly defined in other regions. At Logachev and the HTS, fish community composition varied significantly with both depth and substratum type, with CWCs supporting a significantly different fauna to non-CWC substrata. Single-species analyses of the dominant taxa showed that only *Neocyttus helgae* was significantly more likely to occur with CWCs, while the relative abundances of *Helicolenus dactylopterus, Lepidion eques* (at the HTS only) and *Coryphaenoides rupestris* were significantly affected by depth. These results suggest that CWCs were no more important than other substratum types to most of the dominant taxa observed at the time of this study. These findings are partly supported by Biber et al. (2014) who reported variable relationships between both *L. eques* and *H. dactylopterus* and CWCs and depth in the NE Atlantic. *L. eques* is extremely common in the NE Atlantic and has previously been recorded from numerous locations (e.g. Mauchline and Gordon, 1980; Soeffker et al., 2011), suggesting it may be a highly generalist species in terms of substratum preference. Similarly, *H. dactylopterus* is extremely widespread across the Atlantic generally (Kelly et al., 1999) and was considered a "transient" reef species by Quattrini et al. (2012) rather than a reef-associated one.

Interpreting apparent species-habitat associations must be done with care. It is generally assumed that individuals will select a particular habitat to maximise their success (e.g. Orians and Wittenberger, 1991; Munday, 2001), but benefits can vary both spatially and temporally with both resource availability and the life history stage of the animal (Orians and Wittenberger, 1991; Munday, 2000; Mayor et al., 2009). Drivers of habitat preference cannot be inferred simply from observed distribution patterns, because these do not account for external factors that may constrain habitat choice, such as inter- or intra-specific interactions or other environmental drivers (Auster, 2005). Consequently, any assessment of a species' true preference will require detailed study and experimentation on the organism in question over appropriate temporal and spatial scales. This will prove challenging in the deep sea, but would be beneficial in developing a more complete understanding of the ecological importance of CWCs to deep-sea fish.

While a more detailed understanding of the importance of CWCs to fish may be desirable from a scientific perspective, any such studies are unlikely to produce results for some time. From a management perspective, it may be more prudent in the short-term to adopt a precautionary approach to the spatial

management of deep-water fish, and the results from the present study suggest some possible considerations. While the constraints of the survey methodology mean that the results of the present study should be interpreted cautiously, if MPAs are intended to protect a representative subset of the wider fish community, then our data suggest that they should take account of both broad- and fine-scale spatial drivers of community structure. This would require accounting for the broad-scale effects of depth by selecting an appropriate depth range and then accounting for fine-scale variability within that range by including a sufficient range of substratum types over the spatial scales at which community composition was observed to vary (in this case, at "intermediate" scales of c. 5–50 km). For example, at the Logachev Mounds this may involve protecting a number of coral mounds across their full depth range. The EU fishing closures at Logachev (EC 41/2006; see Fig. 1) may therefore benefit from being extended into shallower depths to include coral mounds occurring at the top of the slope. In the context of the Scottish MPA framework, the proposed MPA at the HTS (JNCC, 2013) should also ensure that a sufficient depth range is covered to include the full range of species encountered, providing that appropriate protection is legislated.

6. Conclusions

Our findings suggest that CWCs support different fish assemblages to non-CWC substrata, but that the precise composition of that assemblage is modified by the broader spatial context, including the effects of depth or the composition of the regional species pool for example. Understanding how different drivers interact to affect the fish fauna across multiple spatial and temporal scales would allow a far greater understanding of the importance of CWCs to different fish and how this may be tied to their life-history traits. The maintenance of natural fish assemblages is nonetheless a valid conservation aim. The precautionary approach would be to assume that CWCs are important areas for the associated fish, and that this should be considered when designing future MPAs. For fish assemblages to be fully protected, MPAs will be needed that encompass both broad- and fine-scale variability by covering a suitable depth range and variety of substrata, including CWC and non-CWC areas. For those species which appear to associate strongly with CWCs (e.g. gravid *Sebastes* sp. 1 at Rockall Bank), it would be prudent to assume that such areas provide "essential habitats" and to manage them accordingly.

Author contributions statement

JMR was principle investigator for the Changing Oceans project and research cruise JC073. Data collection was conducted by RJM and JMR. RJM and GS processed the video data. RJM analysed the results. The main manuscript text, and all tables and figures were prepared by RJM. All authors reviewed the manuscript.

Conflict of interest statement

The authors declare no actual or potential conflicts of interest.

Acknowledgements

The fieldwork supporting this work took place during the 2012 Changing Oceans Expedition (RRS *James Cook* cruise 073) funded by the UK Ocean Acidification Research Programme (Natural Environment Research Council grant NE/H017305/1 to J.M.R.). Supplementary shiptime funding for the ROV seamount surveys was received from the Joint Nature Conservation Committee with the agreement of NERC. Rosanna Milligan was funded by a NERC studentship (NE/I528369). We would like to thank the Captain and crew of the RRS *James Cook*, and the *Holland-1* ROV pilots and technicians who collected the video data, as well as Dr. Paul Johnson (IBAHCM, MVLS, University of Glasgow) for his assistance in developing the GLMMs used to analyse these data.

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.dsr.2016.04.011.

References

Althaus, F., Williams, A., Schlacher, T.A., Kloser, R.J., Green, M.A., Barker, B.A., Bax, N. J., Brodie, P., Schlacher-Hoenlinger, M.A., 2009. Impacts of bottom trawling on deep-coral ecosystems of seamounts are long-lasting. Mar. Ecol. Prog. Ser. 397, 279–294.

Anderson, M.J., 2001. Permutation tests for univariate or multivariate analysis of variance and regression. Can. J. Fish. Aquat. Sci. 58 (3), 626–639.

Anderson, M.J., 2006. Distance-based tests for homogeneity of multivariate dispersions. Biometrics 62 (1), 245–253.

Anderson, T.J., Syms, C., Roberts, D.A., Howard, D.F., 2009. Multi-scale fish-habitat associations and the use of habitat surrogates to predict the organisation and abundance of deep-water fish assemblages. J. Exp. Mar. Biol. Ecol. 379 (1–2), 34–42.

Auster, P.J., 2005. Are deep-water corals important habitats for fishes?. In: Freiwald, A., Roberts, J.M. (Eds.), Cold-Water Corals and Ecosystems, pp. 747–760.

Baillon, S., Hamel, J.-F., Wareham, V.E., Mercier, A., 2012. Deep cold-water corals as nurseries for fish larvae. Front. Ecol. Environ. 10 (7), 351–356.

Baker, K.D., Wareham, V.E., Snelgrove, P.V.R., Haedrich, R.L., Fifield, D.A., Edinger, E. N., Gilkinson, K.D., 2012. Distributional patterns of deep-sea coral assemblages in three submarine canyons off Newfoundland, Canada. Mar. Ecol. Prog. Ser. 445, 235–249.

Bates, D., Meaechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67 (1), 1–48.

Bergstad, O.A., 2013. North Atlantic demersal deep-water fish distribution and biology: present knowledge and challenges for the future. J. Fish Biol. 83 (6), 1489–1507.

Biber, M.F., Duineveld, G.C.A., Lavaleye, M.S.S., Davies, A.J., Bergman, M.J.N., van den Beld, I.M.J., 2014. Investigating the association of fish abundance and biomass with cold-water corals in the deep Northeast Atlantic Ocean using a generalised linear modelling approach. Deep-Sea Res. Part II-Top. Stud. Oceanogr. 99, 134–145.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.-S.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol. Evol. 24 (3), 127–135.

Buckley, J.S., Bailey, R.J., 1975. Geophysical evidence on the nature of the Hebrides Terrace Seamount. Scott. J. Geol. 11, 37–45.

Buhl-Mortensen, L., Vanreusel, A., Gooday, A.J., Levin, L.A., Priede, I.G., Buhl-Mortensen, P., Gheerardyn, H., King, N.J., Raes, M., 2010. Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. Mar. Ecol. Evol. Perspect. 31 (1), 21–50.

Carney, R.S., 2005. Zonation of deep biota on continental margins. In: Gibson, R.N., Atkinson, R.J.A., Gordon, J.D.M. (Eds.), Oceanography and Marine Biology – An Annual Review, Vol. 43, pp. 211.

Chave, J., 2013. The problem of pattern and scale in ecology: what have we learned in 20 years? Ecol. Lett. 16, 4–16.

Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth.

Costello, M.J., McCrea, M., Freiwald, A., Lundalv, T., Jonsson, L., Bett, B.J., van Weering, T.C.E., de Haas, H., Roberts, J.M., Allen, D., 2005. Role of cold-water *Lophelia pertusa* coral reefs as fish habitat in the NE Atlantic. In: Freiwald, A., Roberts, J.M. (Eds.), Cold-Water Corals and Ecosystems, pp. 771–805.

D'Onghia, G., Indennidate, A., Giove, A., Savini, A., Capezzuto, F., Sion, L., Vertino, A., Maiorano, P., 2011. Distribution and behaviour of deep-sea benthopelagic fauna observed using towed cameras in the Santa Maria di Leuca cold-water coral province. Mar. Ecol. Prog. Ser. 443, 95–110.

D'Onghia, G., Maiorano, P., Carlucci, R., Capezzuto, F., Carluccio, A., Tursi, A., Sion, L., 2012. Comparing deep-sea fish fauna between coral and non-coral "mega-habitats" in the Santa Maria di Leuca cold-water coral province (Mediterranean Sea). Plos One 7 (9), e44509.

Davies, A.J., Guinotte, J.M., 2011. Global habitat suitability for framework-forming cold-water corals. Plos One 6, 4.

de Juan, S., Lleonart, J., 2010. A conceptual framework for the protection of

vulnerable habitats impacted by fishing activities in the Mediterranean high seas. Ocean Coast. Manag. 53 (11), 717–723.
Dorschel, B., Wheeler, A.J., Huvenne, V.A.I., de Haas, H., 2009. Cold-water coral mounds in an erosive environmental setting: TOBI side-scan sonar data and ROV video footage from the northwest Porcupine Bank, NE Atlantic. Mar. Geol. 264 (3–4), 218–229.
Drazen, J.C., Haedrich, R.L., 2012. A continuum of life histories in deep-sea demersal fishes. Deep-Sea Res. Part I – Oceanogr. Res. Pap. 61, 34–42.
Du Preez, C., Tunnicliffe, V., 2011. Shortspine thornyhead and rockfish (Scorpaenidae) distribution in response to substratum, biogenic structures and trawling. Mar. Ecol. Prog. Ser. 425, 217–231.
FAO, 2007. Expert Consultation on deep-sea fisheries in the high seas, Bangkok, Thailand, 21–23, November 2006. FAO Fisheries Report (838), pp. vi 203.
FAO, 2009. International Guidelines for the Management of Deep-sea Fisheries in the High Seas. Food and Agriculture Organization of the United Nations,, Rome, p. 73.
Foley, N.S., Kahui, V., Armstrong, C.W., van Rensburg, T.M., 2010. Estimating linkages between redfish and cold water coral on the Norwegian coast. Mar. Resour. Econ. 25 (1), 105–120.
Fosså, J.H., Mortensen, P.B., Furevik, D.M., 2002. The deep-water coral *Lophelia pertusa* in Norwegian waters: distribution and fishery impacts. Hydrobiologia 471, 1–12.
Fournier, D.A., Skaug, H.J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M.N., Nielsen, A., Sibert, J., 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optim. Methods Softw. 27 (2), 233–249.
Freiwald, A., Huhnerbach, V., Lindberg, B., Wilson, J.B., Campbell, J., 2002. The Sula Reef Complex, Norwegian shelf. Facies 47, 179–200.
Gaillard, J.-M., Hebblewhite, M., Loison, A., Fuller, M., Powell, R., Basille, M., Van Moorter, B., 2010. Habitat-performance relationships: finding the right metric at a given spatial scale. Philos. Trans. R. Soc. B Biol. Sci. 365 (1550), 2255–2265.
Hall-Spencer, J., Allain, V., Fosså, J.H., 2002. Trawling damage to Northeast Atlantic ancient coral reefs. Proc. R. Soc. B Biol. Sci. 269 (1490), 507–511.
Henry, L.A., Vad, J., Findlay, H.S., Murillo, J., Milligan, R.J., Roberts, J.M., 2014. Environmental variability and biodiversity of megabenthos on the Hebrides Terrace Seamount (Northeast Atlantic). Sci. Rep. 4 (5589), 1–10.
Howell, K.L., 2010. A benthic classification system to aid in the implementation of marine protected area networks in the deep/high seas of the NE Atlantic. Biol. Conserv. 143 (5), 1041–1056.
Howell, K.L., Davies, J.S., Jacobs, C., Narayanaswamy, B.E., 2009. Broadscale Survey of the Habitats of Rockall Bank and Mapping of Annex I 'Reef' Habitat. JNCC Report. Joint Nature Conservation Committee, Peterborough, p. 244.
Hureau, J.C., 1996. Fishes of the North-eastern Atlantic and the Mediterranean. Windows Version 1.0.
Husebø, A., Nottestad, L., Fosså, J.H., Furevik, D.M., Jorgensen, S.B., 2002. Distribution and abundance of fish in deep-sea coral habitats. Hydrobiologia 471, 91–99.
JNCC, 2013. The Barra Fan and Hebrides Terrace Seamount possible MPA. Scottish MPA Project. Management Options Paper. JNCC, pp. 19.
Kelly, C.J., Connolly, P.L., Bracken, J.J., 1999. Age estimation, growth, maturity, and distribution of the bluemouth rockfish *Helicolenus d. dactylopterus* (Delaroche 1809) from the Rockall Trough. ICES J. Mar. Sci. 56 (1), 61–74.
Kenyon, N.H., Akhmetzhanov, A.M., Wheeler, A.J., van Weering, T.C.E., de Haas, H., Ivanov, M.K., 2003. Giant carbonate mud mounds in the southern Rockall Trough. Mar. Geol. 195 (1–4), 5–30.
Koslow, J.A., 1993. Community structure in north-Atlantic deep-sea fishes. Prog. Oceanogr. 31 (3), 321–338.
Kutti, T., Bergstad, O.A., Fosså, J.H., Helle, K., 2014. Cold-water coral mounds and sponge-beds as habitats for demersal fish on the Norwegian shelf. Deep-Sea Res. Part II-Top. Stud. Oceanogr. 99, 122–133.
Levin, L.A., Etter, R.J., Rex, M.A., Gooday, A.J., Smith, C.R., Pineda, J., Stuart, C.T., Hessler, R.R., Pawson, D., 2001. Environmental influences on regional deep-sea species diversity. Annu. Rev. Ecol. Syst. 32, 51–93.
Levin, S.A., 1992. The problem of pattern and scale in ecology. Ecology 73 (6), 1943–1967.
Mauchline, J., Gordon, J.D.M., 1980. The food and feeding of the deep-sea morid fish *Lepidion eques* (Gunther, 1887) in the Rockall Trough. J. Mar. Biol. Assoc. U. K. 60 (4), 1053–1059.
Mayor, S.J., Schneider, D.C., Schaefer, J.A., Mahoney, S.P., 2009. Habitat selection at multiple scales. Ecoscience 16 (2), 238–247.
Miller, R.J., Hocevar, J., Stone, R.P., Fedorov, D.V., 2012. Structure-forming corals and sponges and their use as fish habitat in Bering Sea submarine canyons. Plos One 7, 3.
Milligan, R.J., Spence, G., Roberts, J.M., Bailey, D.M., 2016. Standardised Abundances of Fish Observed in and Around Cold-water Corals in the North–east Atlantic From Remotely Operated Vehicle (Rov) Observations Made During Cruise JC073. British Oceanographic Data Centre – Natural Environment Research Council, UK.
Morris, D.W., 1987. Ecological scale and habitat use. Ecology 68 (2), 362–369.
Mortensen, P.B., Hovland, M., Brattegard, T., Farestveit, R., 1995. Deep-water bioherms of the scleractinian coral *Lophelia pertusa* (l) at 64 degrees N on the Norwegian shelf – structure and associated megafauna. Sarsia 80 (2), 145–158.
Munday, P.L., 2000. Interactions between habitat use and patterns of abundance in coral-dwelling fishes of the genus *Gobiodon*. Environ. Biol. Fishes 58 (4), 353–369.
Munday, P.L., 2001. Fitness consequences of habitat use and competition among coral-dwelling fishes. Oecologia 128 (4), 585–593.
Norse, E.A., Brooke, S., Cheung, W.W.L., Clark, M.R., Ekeland, L., Froese, R., Gjerde, K. M., Haedrich, R.L., Heppell, S.S., Morato, T., Morgan, L.E., Pauly, D., Sumaila, R., Watson, R., 2012. Sustainability of deep-sea fisheries. Mar. Policy 36 (2), 307–320.
Orians, G.H., Wittenberger, J.F., 1991. Spatial and temporal scales in habitat selection. Am. Nat. 137 (6), 29–49.
Priede, I.G., Godbold, J.A., King, N.J., Collins, M.A., Bailey, D.M., Gordon, J.D.M., 2010. Deep-sea demersal fish species richness in the Porcupine Seabight, NE Atlantic Ocean: global and regional patterns. In: Marine Ecology-an Evolutionary Perspective 31, 1, pp. 247–260.
Quattrini, A.M., Ross, S.W., Carlson, M.C.T., Nizinski, M.S., 2012. Megafaunal-habitat associations at a deep-sea coral mound off North Carolina, USA. Mar. Biol. 159 (5), 1079–1094.
R Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing,, Vienna, Austria.
Rengstorf, A.M., Yesson, C., Brown, C., Grehan, A.J., 2013. High-resolution habitat suitability modelling can improve conservation of vulnerable marine ecosystems in the deep sea. J. Biogeogr. 40 (9), 1702–1714.
Roberts, J.M., 2013. Changing Oceans Expedition 2012. RRS James Cook 073 Cruise Report. Heriot-Watt University, p. 224.
Roberts, J.M., Wheeler, A., Freiwald, A., Cairns, S., Roberts, J.M., Wheeler, A., Freiwald, A., Cairns, S., 2009. Cold-Water Corals: The Biology and Geology of Deep-Sea Coral Habitats. Cambridge University Press, p. 334.
Roberts, J.M., Wheeler, A.J., Freiwald, A., 2006. Reefs of the deep: the biology and geology of cold-water coral ecosystems. Science 312 (5773), 543–547.
Ross, S.W., Quattrini, A.M., 2007. The fish fauna associated with deep coral banks off the southeastern United States. Deep-Sea Res. Part I-Oceanogr. Res. Pap. 54 (6), 975–1007.
Ross, S.W., Quattrini, A.M., 2009. Deep-sea reef fish assemblage patterns on the Blake Plateau (Western North Atlantic Ocean). Mar. Ecol. Evol. Perspect. 30 (1), 74–92.
Soeffker, M., Sloman, K.A., Hall-Spencer, J.M., 2011. In situ observations of fish associated with coral reefs off Ireland. Deep-Sea Res. Part I-Oceanogr. Res. Pap. 58 (8), 818–825.
Stone, R.P., 2006. Coral habitat in the Aleutian Islands of Alaska: depth distribution, fine-scale species associations, and fisheries interactions. Coral Reefs 25 (2), 229–238.
Trenkel, V.M., Lorance, P., Mahevas, S., 2004. Do visual transects provide true population density estimates for deepwater fish? ICES J. Mar. Sci. 61 (7), 1050–1056.
Wilson, J.B., 1979a. The first recorded specimens of the deep-water coral *Lophelia pertusa* (Linnaeus, 1758) from British waters. Bull. Br. Mus. (Nat. Hist.) Zool. 36 (4), 209–215.
Wilson, J.B., 1979b. Patch development of the deep-water coral *Lophelia pertusa* (l) on Rockall Bank. J. Mar. Biol. Assoc. U. K. 59 (1), 165–177.
Wilson, S.K., Burgess, S.C., Cheal, A.J., Emslie, M., Fisher, R., Miller, I., Polunin, N.V.C., Sweatman, H.P.A., 2008. Habitat utilization by coral reef fish: implications for specialists vs. generalists in a changing environment. J. Anim. Ecol. 77 (2), 220–228.